

• Aquatic Biodiversity • AIBS Annual Meeting

# BioScience

Organisms from Molecules to the Environment

October 2006

American Institute of Biological Sciences

Vol. 56 No. 10



**Sexual Conflict and Breeding Systems**

**Fall Focus on Books**

\$5.95 • \$6.95 Canada



[www.biosciencemag.org](http://www.biosciencemag.org)

# Sexual Conflict, Ecology, and Breeding Systems in Shorebirds

TAMÁS SZÉKELY, GAVIN H. THOMAS, AND INNES C. CUTHILL

*Evolutionary biologists strive to understand the immense variation in animals' breeding systems. Shorebirds represent an ideal model system for this endeavor, because they exhibit diverse breeding systems that include monogamy, with the parents cooperating to rear the young; and polygamy by the male, the female, or both parents, with one parent taking full responsibility for incubating the eggs and rearing the young. Recent experimental manipulations, mathematical models, and phylogenetic analyses reveal that evolutionary pressures may diverge as they act on mated pairs of shorebirds, favoring one parent at a cost to the other. We argue that different reproductive payoffs for the male and the female have had fundamental implications for the evolution of diverse breeding systems.*

*Keywords: sexual conflict, breeding system, size dimorphism, polygamy, parental care*

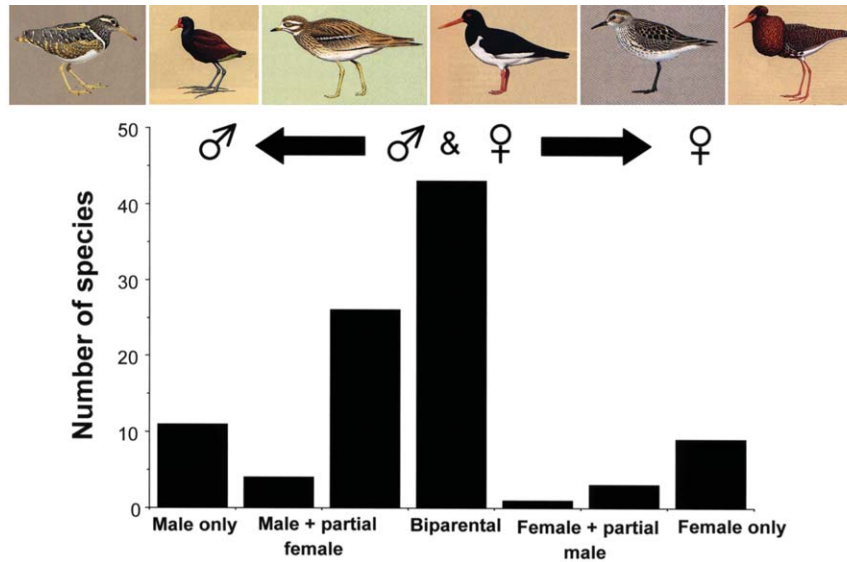
**E**ver since Darwin, shorebirds, or waders (sandpipers, plovers, and allies), have attracted the attention of evolutionary biologists. In his chapter entitled “Law of Battle,” Darwin (1871) used the ruff (*Philomachus pugnax*) to illustrate his theory of sexual selection, noting that the male ruff “is notorious for his extreme pugnacity” in fighting sexual rivals. Darwin also noted that in many shorebird species the usual roles of the sexes are reversed: Female painted snipes (*Rostratula benghalensis*), phalaropes (*Phalaropus* spp.), and dotterels (*Eudromias morinellus*) are “not only larger but much more richly coloured than the males,” and males of these species “shew much greater devotion toward their young...than do females.” Later works confirmed Darwin’s insight (figure 1): Shorebirds do indeed have extremely diverse breeding systems that include polygynous species, such as the ruff, in which males have intense male–male fights and may have several mates simultaneously (or successively); monogamous species in which males and females have comparable roles in mate acquisition, sexual competition, and parental care; and polyandrous species in which the usual sex roles are reversed, with females fighting for males, males providing most of the care for the eggs and young, and some females having more than one male caring for their offspring. This unusual diversity of breeding systems has elicited influential research on sandpipers (Pitelka et al. 1974, Erckmann 1983, Oring and Lank 1986, Lanctot et al. 1997, Lank et al. 2002), jacanas (Emlen and Wrege 2004), and plovers (Owens et al. 1995, Blomqvist et al. 2002).

How did these diverse breeding systems evolve? To answer this question, we use a two-pronged approach. First, we investigate the behavior and ecology of a small,

inconspicuous shorebird (body mass about 42 to 44 grams), the Kentish plover (*Charadrius alexandrinus*; the North American subspecies *C. alexandrinus nivosus* is called the snowy plover), which exhibits a variable breeding system. Although many Kentish plovers are monogamous, so that each plover breeds with only one mate during a breeding season and both parents care for the eggs and young until the chicks fledge, some males and females are sequentially polygamous (Warner et al. 1986, Székely and Lessells 1993), having several mates during one breeding season. Second, we exploit the natural variation in breeding systems among shorebird species, and compare their breeding behavior to their ecology and life history using advanced phylogenetic techniques. The comparative approach, as the latter is often called (Harvey and Pagel 1991, Martins 1996), benefits from the immense “experiment” nature has carried out in producing diverse breeding systems. Researchers studying the results of these natural “experiments” may seek to identify the ecological and life history traits that facilitated the evolution of a particular breeding behavior.

---

*Tamás Székely (e-mail: T.Szekely@bath.ac.uk) works in the Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom. Gavin H. Thomas is with the NERC Centre for Population Biology, Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, United Kingdom. Innes C. Cuthill works in the Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom. © 2006 American Institute of Biological Sciences.*



**Figure 1.** Distribution of parental care in shorebirds. Male-only care is often associated with polyandrous mating systems, whereas female-only care is associated with polygyny and leks (modified from Székely and Reynolds 1995). The species pictured above the graph are, from left to right, the greater painted snipe (*Rostratula benghalensis*), wattled jacana (*Jacana jacana*), Eurasian thick-knee (*Burhinus oedicnemus*), Eurasian oystercatcher (*Haematopus ostralegus*), white-rumped sandpiper (*Calidris fuscicollis*), and ruff (*Philomachus pugnax*); photographs are from del Hoyo and colleagues (1996).

### Family affairs in the Kentish plover

Unlike many species of birds (or mammals for that matter) in which the female bears the brunt of parental care, Kentish plovers of both sexes are fully capable of providing all care for the young. Which parent, if either, should break away from the family, abandoning brood-rearing tasks to seek a new mate?

Evolutionary biologists used to view family life as a mutually beneficial joint effort to produce and rear young. This peaceful view was shattered by the work of Robert Trivers and Geoff Parker, who found that family life is more like a battlefield than a romantic enterprise (Arnqvist and Rowe 2005). Although raising the young is beneficial for both parents if they are equally related to the offspring (as is usually, but not always, the case), the reproductive interests of male and female often diverge. Care is costly to parents because it takes time and energy, and incubating eggs and feeding young may put a parent at risk of predation. Unless the pair is likely to breed together repeatedly in the future, each parent has only short-term interests in its mate's welfare (i.e., for rearing the current brood); these short-term interests may be at odds with long-term interests in securing its own reproductive potential. An outcome of these costs and benefits is that a parent may gain by shunting parental care duties to its mate (Houston et al. 2005).

The antagonistic interests of parents are apparent in the Kentish plover: By deserting the family shortly after the young hatch, one parent avoids the costs of brood rearing and is able to start a new family with a new mate within a few days after desertion. The deserted parent then provides care for the young for about four weeks, until the chicks become fully in-

dependent. The deserted parent accompanies the chicks and broods for extended periods of time (up to 80% of the time with small young), leads them to sites with rich food, defends them from territorial pairs of Kentish plovers that might kill them, and, using distraction displays, leads predators away from the vicinity of the brood. As the costs of brood rearing are great in terms of time lost for producing a new brood, the sexual conflict is over which parent gets to desert.

To find out how Kentish plover parents resolve this conflict, we need to observe families for weeks. This would be a straightforward task in species in which the chicks stay in the nest until they fledge, but plover parents lead the chicks away from the nest scrape shortly after they hatch. The tiny, newly hatched creatures are surprisingly hardy (figure 2a): They can wander over hundreds of meters within only a few hours of hatching, and they are capable of running and swimming long distances (often more than a kilometer) within days. To follow the family movements through salt marsh, sand dunes, ditches, arable land, and lakeshore, we invented a movable blind that is convenient for behavioral observations and is cheap, making it ideal for graduate student research (figure 2b).

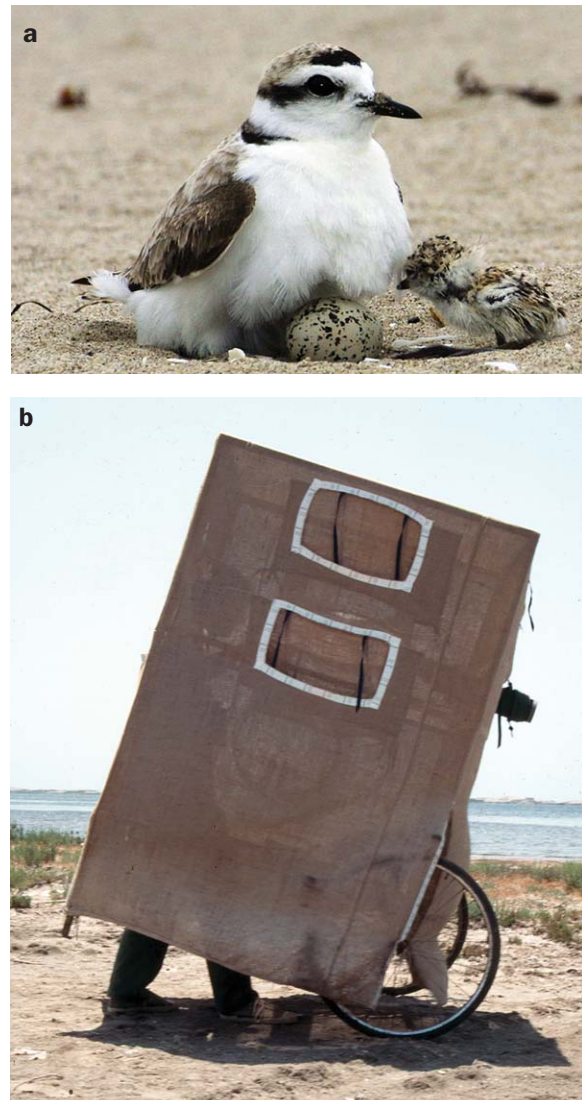
We suspected that the resolution of parental conflict hinges on either the differing parental capabilities of males and females or the differing availabilities of new mates. For example, male shorebirds may, on average, be better parents than females, as Darwin suspected. To test the differing parental capability hypothesis, we experimentally removed one parent (either the male or the female) when the young hatched, to see whether the single father or the single mother did a better job of raising the young to independence (Székely

and Cuthill 1999). We carried out the experiment in a large breeding population of Kentish plovers in southern Turkey, where approximately 1000 pairs of Kentish plovers breed in the salt marsh along Tuzla Lake. Similar experiments have been carried out in many bird species, and the overall conclusion of these experiments is that females are typically better parents than males (Clutton-Brock 1991, Liker 1995). In the Kentish plover, however, we found no difference in the success of chicks raised by a single father or a single mother. Thus, as far as parental abilities are concerned, the cost of desertion for a female plover is no greater than that for a male, because her mate is fully capable of raising the young unassisted.

Alternatively, different mating opportunities for males and females may influence the resolution of the conflict in their long-term interests. For instance, if the females find a new mate sooner than the males, then we would expect females to desert more often than males. In most Kentish plover families the female deserts the brood, and thus we predicted better mating opportunities for the female. We needed an experiment to test this prediction. Simply comparing the mating success of deserting males and females would not reflect the mating potential of an average plover, because the deserters are probably better than average at finding mates.

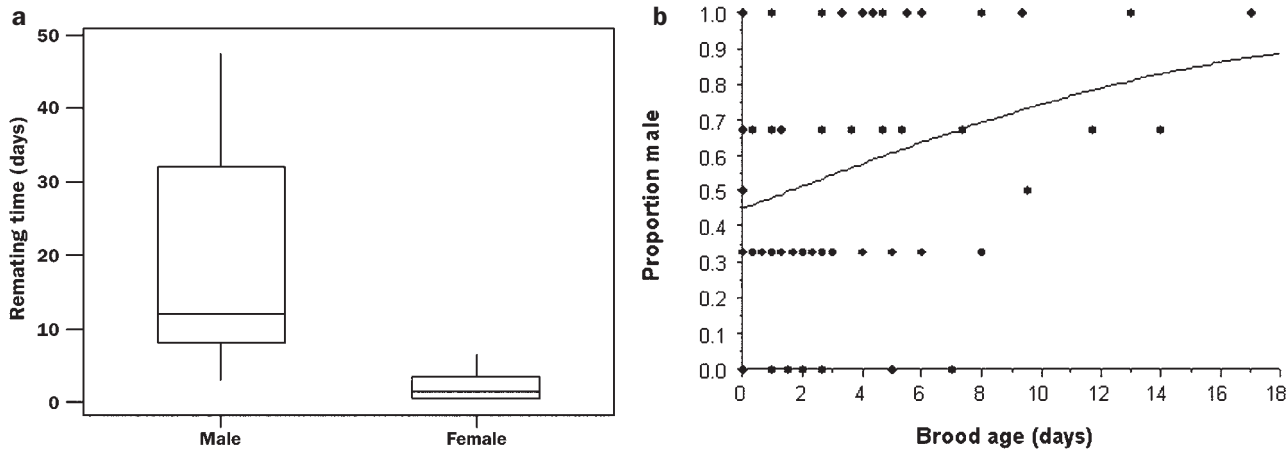
To test the differential mating opportunity hypothesis, we chose mated pairs, trapped either the male or the female, and put him or her in an aviary for a few days near the field site. We then watched how the remaining, “abandoned” bird fared in attracting a new mate. The results were clear-cut: Although males tried hard to attract a new female, it took them more than 12 days, on average, to remate (figure 3a), and some took up to 40 days. Females, on average, remated in less than 2 days. Thus, when it comes to deserting the family, female plovers are at a vast advantage: They can quickly find a new mate, and their former mate is likely to take good care of their offspring.

One of the pinnacles of evolutionary theory is explaining why the sex ratio of many natural populations is approximately equal, 50% males and 50% females. The nearly equal sex ratios of newborn domestic animals had been meticulously noted by Darwin, and the theory of sex ratios was subsequently elaborated by Ronald Fisher, Robert Trivers, and Eric Charnov. The result of our mate removal experiment, however, at first sight seems at odds with sex ratio theory, because the differing time to remating of males and females suggested a bias toward adult males should evolve in the population. We found the adult sex ratio to be significantly male biased over a 10-year period in a small breeding population of Kentish plovers in Sweden (Székely et al. 1999), and Warriner and colleagues (1986) estimated that there were 1.4 adult males for every adult female in a snowy plover population. Male-biased adult sex ratios have been observed in other shorebird species; for instance, in polyandrous wattled jacanas (*Jacana jacana*), there are nearly twice as many males as females (Emlen and Wrege 2004). Thus in the Kentish plover it seems that male-biased sex ratios favor female desertion and polyandry.



**Figure 2.** (a) Male snowy plover with a newly hatched chick. The nest is usually a simple scrape lined with some debris. Photograph: Larry Wan. (b) The movable blind in action. We use these blinds in searching for nests and observing families. The observer can conveniently sit on a bench inside for hours, or push the blind along when a brood is on the move (Székely et al. 2004b). Photograph: Tamás Székely.

How does the male-biased adult sex ratio emerge in a natural population? We pursued two major explanations. First, sex ratio may already be biased by the time the eggs hatch. It is known that sex-ratio distorters (e.g., microbial parasites or so-called meiotic drive genes) may shift sex ratios by selectively eliminating one sex chromosome. However, this explanation is unlikely in the Kentish plover because such sex-ratio distorters have not been reported in birds. Furthermore, when we measured the sex ratio of plover chicks, we found a ratio of nearly one male to one female at hatching (figure 3b).



**Figure 3.** (a) Remating after loss of a mate among Kentish plovers in southern Turkey. We removed one parent (either the male or the female) and then observed the time it took to find a new mate. The females remated more quickly than the males. The boxes show the median, the upper and lower quartile, and the range of data as defined by Székely and colleagues (1999). Used with the permission of Oxford University Press. (b) Sex ratio of Kentish plover broods in southern Turkey. Each dot corresponds to one brood. Older broods have mostly male chicks. The fitted line is from a generalized linear model (Székely et al. 2004c). Used with the permission of Oxford University Press.

Second, males and females may have different mortalities. By collaborating with Brett K. Sandercock at Kansas State University, we compared the mortalities of adult male and female Kentish plovers using powerful statistical tools borrowed from wildlife ecology (Sandercock et al. 2005). To our surprise, adult males and females fared equally well. Chick mortality is severe in many shorebirds, so we wondered whether the mortalities of male and female chicks may differ. The results were striking: As the chicks got older, the brood sex ratio shifted toward males (figure 3b). This shift may be due to actual higher mortality of females or to the disappearance of daughter-dominated broods at young ages. The sex ratio shift toward males is consistent with our mate removal experiment. Nevertheless, this shift is puzzling, because male and female chicks appear to behave the same way and look exactly alike; indeed, we had to use DNA-based tests to sex the chicks. We speculate that females, the heterogametic sex in birds, may be more sensitive to parasites or environmental changes, or perhaps more prone to predation. We are currently testing these alternatives.

The influence of mating opportunities (as a proxy for the adult sex ratio) on breeding systems was confirmed by computer modeling experiments. Working with theoretical biologists (John M. McNamara, Alasdair I. Houston, and James N. Webb at the University of Bristol, Bristol, United Kingdom), we modeled the behavior of a bird population (McNamara et al. 2000). As in our earlier experiment with Kentish plovers, we asked how the adult sex ratio influences parental behavior. In the model (technically known as a state-dependent game-theoretic model) we followed the behavior of mated and unmated birds (with “mated” or “unmated” representing the birds’ state) in a breeding population over a fixed period of time, the breeding season. The “computerized parents” had the option of caring for the young or deserting them, and a

single parent was able to raise several broods within a breeding season. The model sought the evolutionarily stable strategy (ESS), in which the behavior of all individuals in the population is optimal with respect to the others. Finding the ESS for a full population was a challenging task, because the mating and parental behavior of one bird influenced the overall mating opportunities in the population, and the mating opportunities in turn had implications for the optimal mating and parental behavior of a given individual. To tackle this thorny problem, our colleagues invented a new mathematical algorithm to solve complex games, which is based upon errors in decisionmaking (McNamara et al. 1997).

The modeling exercise was rewarding. First, it revealed that the number of mated and unmated birds fluctuated over the breeding season, depending on the time each bird starts and finishes breeding. In addition, the deserting individuals boosted the pool of unmated birds, and this, in turn, induced desertion by the opposite sex. Thus when there was a surplus of unmated females in the population, males started abandoning their mates and their young. Second, the prediction of the ESS model was consistent with our mate removal experiment because, after shifting the adult sex ratio toward males, we observed more brood desertion by females.

### Sexual conflict across phylogeny

Can we detect evidence of sexual conflict using the comparative approach? Our experiments with the Kentish plover and the predictions of the game-theoretic model indicate that an evolutionary tug-of-war exists between males and females over care, consistent with sexual conflict theory (Chapman et al. 2003, Arnqvist and Rowe 2005). If parental conflict is a pervasive evolutionary force, we reasoned that we should see its imprint across the shorebird phylogenetic tree.

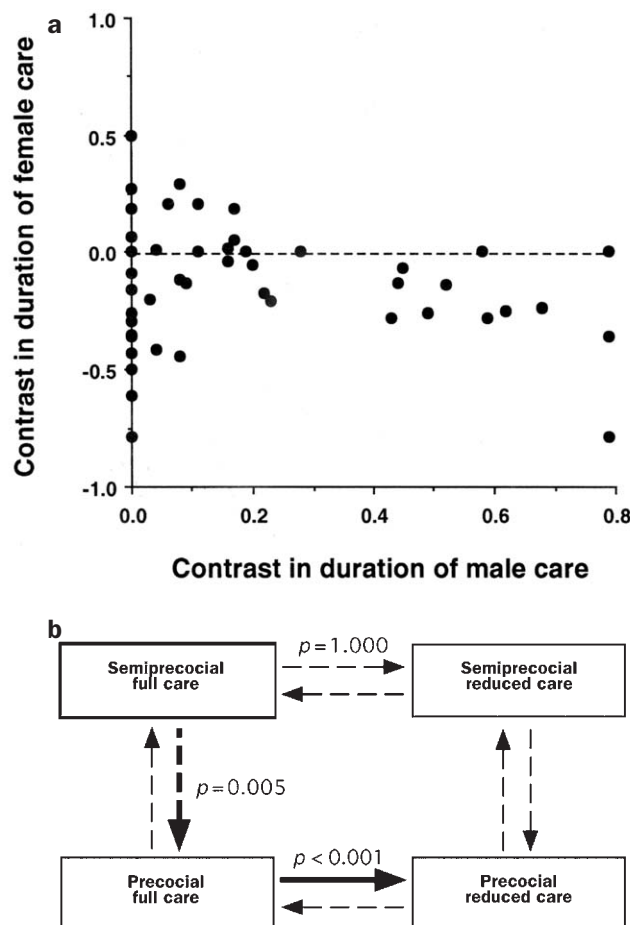
We investigated the evolutionary history of sexual conflict over care using a suite of advanced phylogenetic methods.

For hundreds of years, biologists have based many of their arguments on comparisons of anatomy, development, physiology, and ecology across species. For instance, Darwin extensively used cross-species comparisons to infer the role of sexual selection in the evolution of flashy ornaments and displays. However, closely related species share much of their evolutionary history and as such should not be treated as independent data points—comparative analyses need to take phylogeny into account (Felsenstein 1985). Fortunately, the rapidly increasing number of molecular-based phylogenies (Whittingham et al. 2000, Thomas et al. 2004) makes such analyses possible. In addition, over the last 20 years, comparative biologists have developed powerful statistical models for the reconstruction of trait evolution (Harvey and Pagel 1991, Freckleton et al. 2002).

The first stage in our phylogenetic analyses was to test for evidence of a tug-of-war. We carried out this test by calculating the evolutionary changes in care using the method of phylogenetically independent contrasts (Felsenstein 1985). This method calculates the differences in trait values between sister taxa (either species or nodes within the phylogenetic tree) as weighted by phylogenetic distance between the relatives (Harvey and Pagel 1991). To look for signs of the tug-of-war, we compiled a large data set with John D. Reynolds (then at the University of East Anglia, Norwich, United Kingdom) on breeding systems of shorebirds, and plotted the evolutionary changes (or contrasts) in duration of care between males and females (Reynolds and Székely 1997). It turned out that when males reduced their care the females compensated over evolutionary time, and vice versa, consistent with the tug-of-war hypothesis (figure 4a).

The trade-off between male care and female care raises two questions. First, what limits the intensity of sexual conflict over the care of offspring? In some shorebirds, such as oystercatchers (Haematopodidae) and thick-knees (Burhinidae), the young are fed by the parents, whereas in many others the young require less care; the parents only brood them and defend them from predators. We hypothesized that in those species that have demanding young, the parents would cooperate to raise the young, whereas in shorebirds with less demanding young, there is a potential for parental conflict over care because either parent may desert the brood, as we saw in the Kentish plover.

To test the influences of demanding young on parental conflict over care, first we need to reconstruct the ancestral traits. We used an outgroup comparison to infer ancestral traits; these reconstructions were consistent with fitting a range of evolutionary models and choosing the best-fitting scenario using a maximum likelihood procedure (Thomas and Székely 2005). We inferred that ancestral shorebirds most likely fed their young and that both parents cooperated in raising the chicks. Using these ancestral traits, we used two approaches to test how the feeding behavior of chicks influences parental care strategies. In collaboration with Robert P. Freckleton



**Figure 4. (a) Sexually antagonistic coevolution of parental care in shorebirds. With increasing duration of male care, the duration of female care decreases (binomial test using phylogenetically independent contrasts,  $p < 0.031$ ; Reynolds and Székely 1997). Used with the permission of Oxford University Press. (b) Directional evolution of shorebird chick development from semiprecocial (fed by parents) to precocial (self-feeding) and of parental care from full (biparental) to reduced (uniparental). The thick lines indicate significant transition probabilities ( $p$ ) between reconstructed states. Modified from Thomas and Székely 2005.**

(then at the University of Oxford, Oxford, United Kingdom), we developed a method to test how rates of phenotypic evolution vary between precocial (i.e., independent, self-feeding) and semiprecocial young (i.e., fed by the parents). We showed that biparental care is retained in shorebird species whose young are semiprecocial (Thomas et al. 2006), whereas the breeding systems of precocial shorebirds have diversified rapidly, as predicted by sexual conflict theory, to display a range of parental care strategies including male-only, female-only, and biparental care (see figure 1). Thus it seems that having precocial young opened the possibility for the evolutionary divergence of breeding systems to polygyny and polyandry and

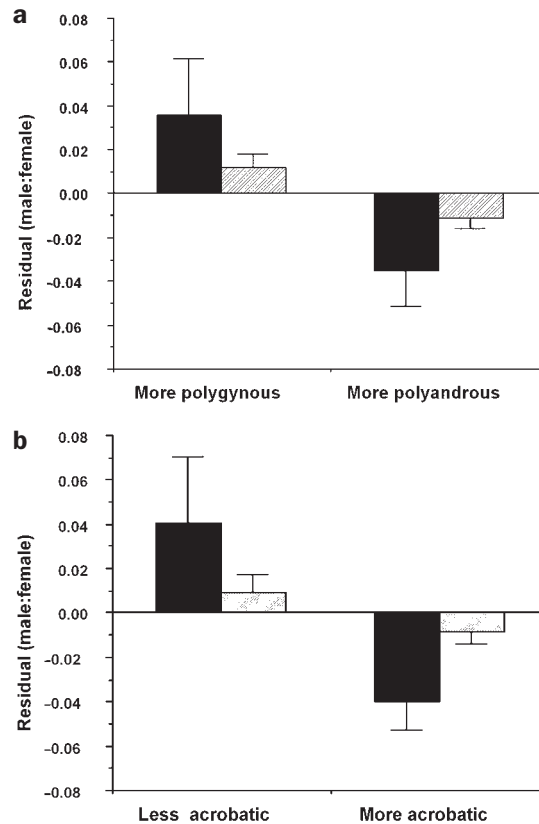
to a system with leks, in which females pick partners at specialized male display sites but, once mated, rear the young unaided.

We then asked whether the evolution of less demanding young relaxed obligate biparental care. The results were highly consistent with our predictions in showing that evolutionary shifts toward precocial young are likely to have preceded changes toward uniparental care (figure 4b). Less demanding young, such as the precocial chicks of many shorebirds, make it possible for one parent to desert and remate (Thomas and Székely 2005).

Our next question was, Why does the male end up providing all the care in some species and the female in others? Comparative analyses identified two likely reasons. The first is linked to mating opportunities. Owens (2002) compared polyandrous avian families to their polygynous relatives and showed that when there are many potential mates for both sexes because the birds breed in high-density groups, polyandry is more likely to evolve than polygyny. The second reason is linked to the fact that many shorebirds are migratory, and travel to their distant wintering grounds often takes a long time and substantial energy. For instance, white-rumped sandpipers (*Calidris fuscicollis*) breed beyond the Arctic Circle in Alaska and Canada and spend the winter in Patagonia. In a pioneering study, Myers (1981) showed that the breeding systems of sandpipers that migrate long distances depart from monogamy. This result was reinforced using phylogenetic contrasts: Longer migratory distance (and most likely earlier departure from breeding ground) was associated with shorter duration of parental care, although this pattern was statistically significant only in females (Reynolds and Székely 1997). We suspect that further advances in comparative analyses of breeding systems and migratory behavior will require better data. For instance, male and female shorebirds of many species spend the nonbreeding season at different latitudes (Nebel et al. 2002), and these differences need to be incorporated into future comparative analyses.

### Sexual conflict and sexual size dimorphism

Sexual conflict over care has profound implications for the sizes of males and females. Differing size of males and females within a species is termed sexual size dimorphism (SSD). Shorebirds exhibit an unusual range of SSD among birds: Male ruffs are about 1.7 times heavier than the females (i.e., male-biased SSD), whereas in the northern jacana (*Jacana spinosa*), the weight of the male is only about 0.6 times that of the female (i.e., female-biased SSD). The selective processes leading to these diverse SSDs are controversial because it is not clear whether selection toward large (or small) size in males, in females, or in both sexes may have produced different optimal sizes for adult males and females (Andersson 1994). One behavior that may contribute to SSD is mating competition, in which the members of one sex compete with each other to gain matings with the other sex. Those shorebird species in which males compete for females usually exhibit male-biased



**Figure 5. Sexual size dimorphism in shorebirds in relation to (a) the intensity of sexual competition and (b) the agility of male displays. Bars above the line indicate male-biased dimorphism in body mass (filled) or wing length (hatched), whereas bars below the line indicate female-biased dimorphism (mean  $\pm$  standard error; further details are in Székely et al. 2000). Reprinted from *Evolution* and used with the permission of the Society for the Study of Evolution.**

SSD, whereas those species in which females compete for males often have female-biased dimorphism (figure 5a).

The story of sexual conflict and SSD, however, has two surprising twists. First, in some shorebirds, including many sandpipers and snipes, the males display acrobatically while fighting over mates, or perhaps to attract females (Jehl and Murray 1986). These agile displays include steep dives and acrobatic zigzagging. Other shorebirds, notably ruffs, jacanas, avocets, and thick-knees, display mostly on the ground, and without acrobatic maneuvers. Flight mechanical theory predicts that maneuverability decreases with body size, so that in acrobatic shorebirds we expect males to be small relative to females. This is clearly the case (figure 5b).

Second, the influences of sexual competition and display agility are interactive; thus shorebirds with intense male–male competition tend to exhibit male-biased SSD if males have terrestrial displays and female-biased SSD if males have agile aerial displays. The statistical interaction between male–male competition and display agility explains the

existence of a common allometric relationship between the sizes of males and females. Bernhard Rensch, a German evolutionary biologist, noted that the sizes of males change more than the sizes of females across species. Primates, hummingbirds, lizards, and water striders exhibit this pattern, termed “Rensch’s rule” by Fairbairn (1997). SSD in shorebirds is also consistent with Rensch’s rule (Székely et al. 2004a).

Our comparative analyses suggest that the intensity of competition between male shorebirds forces the relationship between male and female size away from unity, with the direction of the shift depending on the agility of male displays. If males evolve agile displays, then male sizes are likely to fall below the sizes of females, whereas in nonagile shorebirds for which power and thus sheer body mass matter, males are likely to be larger than females. Male agility also predicted SSD in bustards (Otididae), independent from the influence of mating competition (Raihani et al. 2006). We suspect that the selective advantage of small, maneuverable males may be a hitherto neglected selective process that operates in many species in which agility is important: Bats, primates, seals, and hummingbirds appear to be excellent groups to test the male agility hypothesis in the context of SSD.

## Conclusions

Our quest to understand breeding systems of shorebirds has produced novel insights into breeding system evolution. First, we discovered that population sex ratio influences parental behavior via mating opportunities. Second, we spotted the imprints of the tug-of-war over the care of progeny between males and females: When one sex puts less effort into raising young, the other must make up the loss. Finally, en route to understanding the evolution of breeding systems using conflict and cooperation between parents as a guiding principle, we and our colleagues invented a suite of new techniques, including a movable blind, a mathematical solution for dynamic games, and a phylogenetic method to compare phenotypic rates of evolution between lineages.

The quest, however, is far from complete. First, we have much to discover about why and how population sex ratios are maintained and regulated in nature. This is a vast task, given the mobility of many shorebirds, which may wander over hundreds of kilometers in search of mates. For instance, plovers were observed and suspected to breed within a single breeding season at sites that are 660 km and 170 km apart in California and Hungary, respectively (Székely and Lessells 1993, Stenzel et al. 1994). Second, we need to grasp better how breeding systems function in nature. For instance, if a youngster is reared in a father-only family, will this influence how it will behave in its own family? Third, although we assume, along with most researchers, that the deserted parent loses by taking up the brunt of care, the deserted parent may also gain benefits that merit investigation. For example, the attractiveness of the deserted parent to potential future mates may be increased by the demonstration that it is a competent parent. We noted in our fieldwork that female Kentish plovers were unusually receptive to the courtship of

males caring for nearly fledged and apparently healthy chicks. Finally, about half of shorebird populations are declining across the globe, and many of them are endangered. It is a major task to reveal why these populations are declining, and flexibility (or inflexibility) in breeding systems may partly hold the answer. We strongly believe that our experimental, modeling, and phylogenetic studies that were driven by evolutionary questions will ultimately advance conservation for the benefit of shorebirds.

## Acknowledgments

Funding for this project was provided by the Natural Environment Research Council (GR3/10957) and the Biotechnology and Biological Sciences Research Council (BBS/B/05788). T. S. was also supported by a Leverhulme Trust Research Fellowship during the write-up. Two anonymous referees, Patty Gowaty, Brett Sandercock, and John Reynolds provided valuable comments for the article’s revision. Finally, we thank the many colleagues and students who have contributed to this research.

## References cited

- Andersson M. 1994. *Sexual Selection*. Princeton (NJ): Princeton University Press.
- Arnqvist G, Rowe L. 2005. *Sexual Conflict*. Princeton (NJ): Princeton University Press.
- Blomqvist D, Andersson M, Küpper C, Cuthill IC, Kis J, Lanctot RB, Sandercock BK, Székely T, Wallander J, Kempenaers B. 2002. Genetic similarity between mates explains extra-pair parentage in three species of waders. *Nature* 419: 613–615.
- Chapman T, Arnqvist G, Bangham J, Rowe L. 2003. Sexual conflict. *Trends in Ecology and Evolution* 18: 41–47.
- Clutton-Brock TH. 1991. *The Evolution of Parental Care*. Princeton (NJ): Princeton University Press.
- Darwin C. 1871. *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- del Hoyo J, Elliott A, Sargatal J, eds. 1996. *Handbook of the Birds of the World*, vol. 3: Hoatzin to Auks. Barcelona (Spain): Lynx Edicions.
- Emlen ST, Wrege PH. 2004. Size dimorphism, intrasexual competition, and sexual selection in wattled jacana (*Jacana jacana*), a sex-role reversed shorebird in Panama. *The Auk* 121: 391–403.
- Erckmann WJ. 1983. The evolution of polyandry in shorebirds: An evaluation of hypotheses. Pages 113–168 in Wasser SK, ed. *Social Behavior of Female Vertebrates*. New York: Academic Press.
- Fairbairn DJ. 1997. Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. *Annual Reviews in Ecology and Systematics* 28: 659–687.
- Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* 125: 1–15.
- Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist* 160: 712–726.
- Harvey P, Pagel MD. 1991. *The Comparative Method in Evolutionary Biology*. Oxford (United Kingdom): Oxford University Press.
- Houston AI, Székely T, McNamara JM. 2005. Conflict over parental care. *Trends in Ecology and Evolution* 20: 33–38.
- Jehl JR, Murray BG. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Current Ornithology* 3: 1–86.
- Lanctot RB, Scribner KT, Kempenaers B, Weatherhead PJ. 1997. Lekking without a paradox in the buff-breasted sandpiper. *American Naturalist* 149: 1051–1070.

- Lank DB, Smith CM, Hanotte O, Ohtonen A, Bailey S, Burke T. 2002. High frequency of polyandry in a lek mating system. *Behavioral Ecology* 13: 209–215.
- Liker A. 1995. Monogamy in precocial birds: A review. *Ornis Hungarica* 5: 1–14.
- Martins EP. 1996. *Phylogenies and the Comparative Method*. New York: Oxford University Press.
- McNamara JM, Webb JN, Collins EJ, Székely T, Houston AI. 1997. A general technique for computing evolutionarily stable strategies based on errors in decision-making. *Journal of Theoretical Biology* 189: 211–225.
- McNamara JM, Houston AI, Székely T, Webb JN. 2000. A dynamic game-theoretic model of parental care. *Journal of Theoretical Biology* 205: 605–623.
- Myers JP. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behavioral Ecology and Sociobiology* 8: 195–202.
- Nebel S, et al. 2002. Western sandpipers (*Calidris mauri*) during the non-breeding season: Spatial segregation on a hemispheric scale. *The Auk* 119: 922–928.
- Oring LW, Lank DB. 1986. Polyandry in spotted sandpipers: The impact of environment and experience. Pages 21–42 in Rubenstein DI, Wrangham RW, eds. *Ecological Aspects of Social Evolution*. Princeton (NJ): Princeton University Press.
- Owens IPF. 2002. Male-only care and classical polyandry in birds: Phylogeny, ecology and sex differences in remating opportunities. *Philosophical Transactions of the Royal Society B* 357: 283–293.
- Owens IPF, Dixon A, Burke T, Thompson DBA. 1995. Strategic paternity assurance in the sex-role reversed Eurasian dotterel (*Charadrius morinellus*): Behavioral and genetic evidence. *Behavioral Ecology* 6: 14–21.
- Pitelka FA, Holmes RT, Maclean SF. 1974. Ecology and evolution of social organization in Arctic sandpipers. *American Zoologist* 14: 185–204.
- Raihani G, Székely T, Serrano-Meneses MA, Pitra C, Goriup P. 2006. The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Animal Behaviour* 71: 833–838.
- Reynolds JD, Székely T. 1997. The evolution of parental care in shorebirds: Life histories, ecology and sexual selection. *Behavioral Ecology* 8: 126–134.
- Sandercock BK, Székely T, Kosztolányi A. 2005. The effects of age and sex on the apparent survival of Kentish plovers breeding in southern Turkey. *The Condor* 107: 582–595.
- Stenzel LE, Warriner JC, Warriner JS, Wilson KS, Bidstrup FC, Page GW. 1994. Long-distance breeding dispersal of snowy plovers in western North America. *Journal of Animal Ecology* 63: 887–902.
- Székely T, Cuthill IC. 1999. Brood desertion in Kentish plover: The value of parental care. *Behavioral Ecology* 10: 191–197.
- Székely T, Lessells CM. 1993. Mate change by Kentish plovers *Charadrius alexandrinus*. *Ornis Scandinavica* 24: 317–322.
- Székely T, Reynolds JD. 1995. Evolutionary transitions in parental care in shorebirds. *Proceedings of the Royal Society B* 262: 57–64.
- Székely T, Cuthill IC, Kis J. 1999. Brood desertion in Kentish plover: Sex differences in remating opportunities. *Behavioral Ecology* 10: 185–190.
- Székely T, Reynolds JD, Figuerola J. 2000. Sexual size dimorphism in shorebirds, gulls and alcids: The influence of sexual and natural selection. *Evolution* 54: 1404–1413.
- Székely T, Freckleton RP, Reynolds JD. 2004a. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences* 101: 12224–12227.
- Székely T, Kis J, Kosztolányi A. 2004b. Using a mobile hide in wader research. *Wader Study Group Bulletin* 103: 40–41.
- Székely T, Cuthill IC, Yezerinac S, Griffiths R, Kis J. 2004c. Brood sex ratio in the Kentish plover. *Behavioral Ecology* 15: 58–62.
- Thomas GH, Székely T. 2005. Evolutionary pathways in shorebird breeding systems: Sexual conflict, parental care and chick development. *Evolution* 59: 2222–2230.
- Thomas GH, Wills MA, Székely T. 2004. Phylogeny of shorebirds, gulls and alcids (Aves: Charadrii) from the cytochrome-b gene: Parsimony, quartet puzzling and Bayesian inference. *Molecular Phylogenetics and Evolution* 30: 516–526.
- Thomas GH, Freckleton RP, Székely T. 2006. Comparative analyses of the influence of developmental mode on phenotypic diversification rates in shorebirds. *Proceedings of the Royal Society B* 273: 1619–1624.
- Warriner JS, Warriner JC, Page GW, Stenzel LE. 1986. Mating system and reproductive success of a small population of polygamous snowy plovers. *Wilson Bulletin* 98: 15–37.
- Whittingham LA, Sheldon FH, Emlen ST. 2000. Molecular phylogeny of jacanas and its implications for morphologic and biogeographic evolution. *The Auk* 117: 22–32.